

Optimal allocation strategies and optimal seed mass of a perennial plant

Andrii Mironchenko

*Institute of Mathematics, University of Würzburg, Emil-Fischer Straße 40, 97074
Würzburg, Germany*

Abstract

In this paper we propose a novel optimal allocation problem for perennial plants. We do not restrict ourselves to consider only the periods favorable for photosynthesis, but analyze the whole life period of a perennial plant. This provides more information about the strategies of a plant during transitions between the favorable and unfavorable seasons. One of predictions of the model is that a plant can begin re-establishment of vegetative tissues some time before the beginning of the favorable conditions, so as to come into the better environmental conditions with a certain amount of already developed vegetative tissues.

In the second part of the paper we extend the model developed in previous sections to the case, when a plant controls not only a distribution of allocated carbohydrates, but also a size of a seed. We provide sufficient conditions under which the optimal strategy for a plant is to produce as much seeds as possible. These results can be applied in particular for colonizing species and plants living in open environments. The opposite strategy, namely to produce the seeds as large as possible, is also considered.

Keywords: optimal phenology; size-number trade-off; biomass partitioning; perennial plants

Email address: `andrii.mironchenko@mathematik.uni-wuerzburg.de` (Andrii Mironchenko)

1. Introduction

The pioneering work [1] gave rise to a new class of mathematical models of plants, based on the methods of optimal control theory in which it is assumed that a plant can control itself to maximize its fitness to environment which is often identified with the mass of seeds produced by a plant during its life.

The first models have been devoted to the development of annual plants. In them it is assumed that a plant consists of a number of compartments, at least of vegetative compartment (leaves, roots, stems) and reproductive compartment (seeds and auxiliary tissues), but also can include storage and defensive tissues.

The basic model of this type [2] results in a bang-bang transition from the allocation to vegetative tissues to the allocation to seeds.

This model of an annual plant has been extended in many directions: in particular in [3] a model with multiple vegetative compartments has been analyzed, in works [4], [5] a model with additional physiological constraints has been considered that results in periods of mixed growth (where both vegetative and reproductive parts of a plant grow simultaneously). The optimal allocation strategies in stochastic environments have been investigated in particular in [6]. Allocation to defensive tissues was encountered, to cite a few, in [7], [8].

The overview of the early works in this field is provided in a paper [9]. For general overview of the resource allocation in plants see books [10] and [11].

In contrast to annual plants, to the modeling of optimal phenology of perennials less attention was devoted. Usually behavior of perennials is modeled in the following way [12], [13], [14]: the life-time of a perennial plant is divided into discrete seasons, which environmental conditions are favorable to the photosynthesis. The model of a plant in every season is continuous and is treated with the methods used in annual plant models. To model the behavior of a plant between seasons (when the weather is unfavorable) some simple transition rules are used that show which parts of compartments are saved during the season and which are not.

The solution of such problems is divided into two parts: firstly the model on one season is solved using Pontryagin's Maximum Principle (see, e.g. [15]) and then one seeks a solution of the whole model using dynamic programming method.

Although these models provide quite interesting qualitative results of be-

havior of perennial plants, they have an important disadvantage: a subtle qualitative behavior of a plant within the season contrasts to the simple jump from the end of one season to the beginning of the next one.

In this paper we are going to propose a continuous-time model of a perennial plant. This allows us to describe more precisely the dynamics of a plant during seasons with unfavorable for photosynthesis environmental conditions and to avoid the introduction of additional parameters for description of jumps between seasons.

In particular one of predictions of the model is that the plant begins to generate the vegetative tissues not at the time, when the environment conditions are favorable for photosynthesis, but some time before, so as to come into the suitable period with developed vegetative tissues.

In the second part of the paper we investigate a trade-off between size and number of seeds. A lot of attention is devoted to this topic in the scientific literature. The basic model has been proposed in a seminal work [16], where it was assumed that the fitness of the plant is equal to the sum of the fitnesses of the descendants. Since that this model has been generalized in many directions (for a review see [17]). In this framework the optimal size is sought depending on the properties of the fitness function. This makes possible quite general treatment of size-number trade-offs, but the question remains, how to formalize the dependency of the fitness on size and number of seeds and how to find the properties of the function, that characterizes this dependency.

Our aim is to investigate the trade-offs between number and size of a seed in the context of the optimal allocation models. Within this framework the fitness is properly formalized, and we can investigate the optimal size of a seed depending on the properties of photosynthetic rate function, and other physiological parameters of a plant that are more distinct criteria than the abstract fitness. We provide the analysis for the model developed in Section 2 of this paper, but the results are valid also for a number of other optimal allocation models.

We prove that, according to our model of a plant, if the photosynthetic rate function is concave (that is, if rate of photosynthesis per unit mass decays with increase of a size of a plant), then the seeds have to be as small as possible. This behavior is usual in particular for the colonizing species (see Section 3.2).

Our model includes also the possibility of choosing of a sprouting time by a seed. As a consequence we obtain the results, concerning qualitative

behavior of a plant from the dormancy up to senile stage.

The outline of the article is as follows: in Section 2.1 we introduce the model of a perennial plant. In Section 2.2 we provide its analysis, using Pontryagin's Maximum Principle. Then, in Section 2.3 we summarize the results of the model, provide a general scheme of plant development and consider some special cases (annual and monocarpic plants).

In Section 3 we consider a trade-off between size and number of seeds. The results of the paper are discussed in the Section 3.2. Section 4 concludes the paper.

2. Model, in which a plant controls the free carbonates

2.1. Model description

Usually it is assumed that all the allocated photosynthate is immediately used for construction of the tissues. In the models, taking into account a presence of a storage compartment, a plant can also allocate the resources from the storage with some maximal rate (depending on the mass of the storage).

Such a method ignores that a photosynthate is not immediately allocated to certain structures, but exists for some time in the free state. We are going to take this effect into account and assume that there exists an intermediate stage, when the carbohydrates have already been photosynthesized, but have not already been permanently allocated to a given structure.

Let a plant consist of three parts: vegetative compartment, reproductive compartment and nonstructural carbohydrates (free glucose, starch etc.). Let $x_1(t)$ be the mass of vegetative compartment at time t , $x_2(t)$ be the mass of reproductive compartment at time t , $x_3(t)$ be the mass of nonstructural carbohydrates at time t .

We model dynamics of a plant by the following equations:

$$\begin{cases} \dot{x}_1 = v_1(t)g(x_3) - \mu(t)x_1, \\ \dot{x}_2 = (v(t) - v_1(t))g(x_3), \\ \dot{x}_3 = \nu(t)f(x_1) - v(t)g(x_3) - \omega(t)x_3. \end{cases} \quad (1)$$

Here $f(x_1)$ shows the rate of photosynthesis of the plant with the vegetative mass x_1 in the optimal environmental conditions, and $g(x_3)$ - the maximal rate of allocation of nonstructural carbohydrates. It is natural to assume that f and g are monotonically increasing and $f(0) = g(0) = 0$.

The influence of a climate is modeled by three functions: $\nu : [0, T] \rightarrow [0, 1]$ and $\mu, \omega : [0, T] \rightarrow [0, \infty)$.

$\nu(t)$ shows the dependence of the rate of photosynthesis on the climate ($\nu(t) = 0$ if at time t no photosynthesis is possible).

$\mu(t)$ is the deconstruction rate of vegetative tissues per unit mass at time t

$\omega(t)$ is the deconstruction rate due to external factors (spoiling, grazing by animals etc.) of the storage parts per unit mass at the time t .

Note that photosynthesized carbohydrates firstly enlarge the mass of non-structural carbohydrates.

We assume that a plant can control the total allocation rate with the control $v(t) \in [0, 1]$, and allocation rate to the vegetative tissues $v_1(t) \in [0, v(t)]$, consequently the allocation rate to reproductive tissues at time t is $v_2(t) = v(t) - v_1(t)$.

At the moment $t = 0$ a mass of the seed and all its compartments is given a priori (the question of optimal mass of a seed will be considered in the next section):

$$x_i(0) = x_i^0, \quad i = 1, 2, 3. \quad (2)$$

The seed dormancy is modeled as an ability of a plant to choose the time of sprouting $t_0 \in [0, T]$. For simplicity we assume that a seed cannot spoil, and it does not use any resources for life-sustaining activities, thus:

$$x_i(t_0) = x_i(0) = x_i^0, \quad i = 1, 2, 3. \quad (3)$$

As the aim of a plant we choose maximization of the total yield of seeds over the period:

$$x_2(T) \rightarrow \max. \quad (4)$$

A plant can achieve this aim choosing the appropriate sprouting time t_0 and controls v and v_1 defined on $[t_0, T]$.

We assume that the functions in the right hand side of equations (1) are smooth enough to guarantee existence and uniqueness of solutions of (1). Also we assume that the system (1) is forward complete, that is, for all initial conditions and all admissible controls the solutions of (1) exists for all time. From the biological viewpoint it means that it is impossible to achieve endless yield in finite time. This assures that the solution of the problem (1), (2), (4) exists.

2.2. Model analysis

For analysis we exploit Pontryagin's Maximum Principle (see, e.g. [15]). The Hamiltonian of the system (1) is defined by:

$$H = p_1 (v_1(t)g(x_3) - \mu(t)x_1) + p_2 (v(t) - v_1(t))g(x_3) + p_3 (\nu(t)f(x_1) - v(t)g(x_3) - \omega(t)x_3). \quad (5)$$

Functions p_1, p_2, p_3 are so-called adjoint functions. The equations determining their dynamics will be given later. We rewrite expression (5) in a more suitable form

$$H = p_3\nu(t)f(x_1) - p_1\mu(t)x_1 + g(x_3)(v_1(t)(p_1 - p_2) + v(t)(p_2 - p_3)) - p_3\omega(t)x_3. \quad (6)$$

For computing of the boundary values of functions p_i , $i = 1, \dots, 3$ the following function is needed

$$l(t_0, x(t_0), x(T)) = -\lambda_0 x_2(T) + \sum_{i=1}^3 \lambda_i (x_i(t_0) - x_0^i) + \lambda_4 t_0. \quad (7)$$

Here $\lambda_0 \geq 0$, $\lambda_4 \leq 0$, $\lambda_i \in \mathbb{R}$, $i = 1, 2, 3$.

Equations for the adjoint function p are as follows

$$\begin{cases} \dot{p}_1 = p_1\mu(t) - p_3\nu(t)\frac{\partial f}{\partial x_1}(x_1), \\ \dot{p}_2 = 0, \\ \dot{p}_3 = -\frac{\partial g}{\partial x_3}(x_3)(v_1(p_1 - p_2) + v(p_2 - p_3)) + p_3\omega(t). \end{cases} \quad (8)$$

The corresponding boundary conditions are

$$\begin{cases} p_1(T) = 0, \\ p_2(T) = \lambda_0, \\ p_3(T) = 0. \end{cases} \quad (9)$$

Initial conditions are

$$p_i(t_0) = \frac{\partial l}{\partial x_i(t_0)} = \lambda_i, \quad i = 1, 2, 3. \quad (10)$$

Possibility to choose optimal t_0 provides us with one more equation

$$H(t_0) = -\frac{\partial l}{\partial t_0} = -\lambda_4. \quad (11)$$

Also the condition of complementary slackness must hold

$$\lambda_4 \cdot t_0 = 0. \quad (12)$$

To obtain the values of v, v_1 , we solve the problem

$$H \rightarrow \max, \quad 0 \leq v \leq 1, \quad 0 \leq v_1 \leq v.$$

It is not hard to check that its solution is given by

1. If $p_2 - p_3 > 0$, then $v = 1$, and

$$v_1 = \begin{cases} v & \text{if } p_1 - p_2 > 0, \\ 0 & \text{if } p_1 - p_2 < 0, \\ \in [0, v] & \text{if } p_1 - p_2 = 0. \end{cases} \quad (13)$$

2. If $p_2 - p_3 = 0$, then

$$\begin{aligned} p_1 - p_2 > 0 &\Rightarrow v = 1, v_1 = v \\ p_1 - p_2 = 0 &\Rightarrow v, v_1 - \text{every possible controls} \\ p_1 - p_2 < 0 &\Rightarrow v - \text{every possible control}, v_1 = 0 \end{aligned} \quad (14)$$

3. If $p_2 - p_3 < 0$, then

- if $p_1 - p_2 \leq 0$ then $v = v_1 = 0$.
- if $p_1 - p_2 > 0$ then

$$\begin{aligned} p_1 - p_3 < 0 &\Rightarrow v = v_1 = 0 \\ p_1 - p_3 = 0 &\Rightarrow v - \text{every possible control}, v_1 = v \\ p_1 - p_3 > 0 &\Rightarrow v = v_1 = 1 \end{aligned} \quad (15)$$

We introduce three main periods characterized by different values of controls:

1. Vegetative period: $p_1 > \max\{p_2, p_3\}$. In this case $v = v_1 = 1$, that is the vegetative parts are being constructed with maximal rate.
2. Reproductive period: $p_2 > \max\{p_1, p_3\}$. In this case $v = 1, v_1 = 0$ and reproductive tissues are being constructed with maximal rate.
3. Storage period: $p_3 > \max\{p_1, p_2\}$. In this case $v = v_1 = 0$ and new tissues are not being constructed.

We are going to analyze these periods more deeply and find out in what order these periods can arise in a life of a plant. To this end we investigate equations (8) from the end of the life of a plant.

If $\lambda_0 = 0$, then from (9) and (8) we obtain that $p_i \equiv 0$ on $[t_0, T]$, from which it follows that all the controls are possible.

Let $\lambda_0 > 0$. We can take in this case $\lambda_0 = 1$.

Controls v and v_1 maximize the value of $(v_1(p_1 - p_2) + v(p_2 - p_3))$, therefore for optimal v, v_1 it holds that

$$(v_1(p_1 - p_2) + v(p_2 - p_3)) \geq 0. \quad (16)$$

Note that in case, when $\omega(t) \equiv 0$ (that is, if storage parts cannot be destructed due to external factors) this inequality and monotonicity of g imply that p_3 is a non-increasing function on $[t_0, T]$.

Let us analyze the behavior of Lagrange multipliers p_i and values of controls at the neighborhood of the time T .

From conditions (9) we see that at the moment $t = T$ it holds $p_2(T) > \max\{p_1(T), p_3(T)\}$ and from continuity of p_i , $i = 1, 2, 3$ it follows that the last period of the plant life is always a reproductive period.

From equations (16) and (8) using monotonicity of g and inequality $\omega \geq 0$ we have that if for some $\tau \in [t_0, T]$ $p_3(\tau) < 0$, then $p_3(t) < 0$ for all $t \in [\tau, T]$, which contradicts to (9). Thus, $p_3 \geq 0$ on $[t_0, T]$. Analogously one can prove that $p_1 \geq 0$ on $[t_0, T]$.

During a reproduction period equations (8) after substitution of corresponding controls take a form

$$\begin{cases} \dot{p}_1 = p_1(t)\mu(t) - p_3(t)\nu(t)\frac{\partial f}{\partial x_1}(x_1(t)), \\ \dot{p}_2 = 0, \\ \dot{p}_3 = -\frac{\partial g}{\partial x_3}(x_3(t))(p_2(t) - p_3(t)) + \omega(t)x_3(t). \end{cases} \quad (17)$$

From these equations it follows that

$$\sup\{\tau \in [0, T] : p_1(\tau) = p_2(\tau)\} \geq \sup\{\tau \in [0, T] : p_3(\tau) = p_2(\tau)\}.$$

This tells us that before reproduction period the storage period is impossible. Let t_1 be the last (nearest to T) moment, such that $p_1(t_1) = p_2(t_1)$.

If the climate conditions (functions μ and ν) are such that $p_1(t) = p_2(t)$ for all $t \in [t_s, t_1]$ for some $t_s < t_1$, then according to (13) plant can have the period with mixed control $v_1 \in [0, v]$ for $t \in [t_s, t_1]$. Although this possibility

cannot be excluded in general, but such mixed controls can arise only due to very specific climate conditions and we do not separate it as a special period of plant life.

If p_1 is increasing at $t = t_1$, then one can distinguish one more reproductive period $[t_1 - s, t_1)$ for some $s > 0$. Throughout this paper we follow the agreement to combine all such periods together with stages with mixed controls between these periods into one reproductive period.

Let p_1 be decreasing. Then for some time interval preceding to the reproductive period we have $p_1 > p_2 > p_3$ and therefore on this time interval a plant has a vegetative period. We will call it period 1.1, in contrast to 1.2 characterized by relation $p_1 > p_3 > p_2$ (this distinction is useful for monocarpic plants).

Equations (8) in the vegetative period take form:

$$\begin{cases} \dot{p}_1 = p_1(t)\mu(t) - p_3(t)\nu(t)\frac{\partial f}{\partial x_1}(x_1(t)), \\ \dot{p}_2 = 0, \\ \dot{p}_3 = -\frac{\partial g}{\partial x_3}(x_3(t))(p_1(t) - p_3(t)) + \omega(t)x_3. \end{cases} \quad (18)$$

There are 2 possibilities for the plant behavior before period 1: either it will have one more 0-th period (if p_1 decreases lower than p_2 while it remains true that $p_3 < p_2$), or it will exist $t_2 < t_1$: $p_3(t_2) = p_2(t_2)$. As mentioned before, we neglect the possibility of mixed controls and consider the case $\dot{p}_3(t_2) < 0$.

In this case period 1.2 characterized by $p_1 > p_3 > p_2$ precedes the period 1.1.

To understand the difference between periods 1.2 and 1.1, let us consider the case, when $\omega \equiv 0$ (which implies, as was mentioned earlier, that p_3 is non-increasing). This implies that before period 1.2 the reproduction periods are not possible ($p_3 > p_2$) and consequently *the plant exploits monocarpic strategy*.

In more general case, when $\omega \neq 0$ both periods 2 and 3 can precede the first period, or all the previous life of a plant can consist of one vegetative period. In the first case a plant possesses one more reproduction period, which has been already analyzed. If before vegetative period there is no other period, then the *plant is annual*.

Let now the third period precedes to the first one. Then there exist t_4, t_3 : $t_4 < t_3 < t_2$, such that p_1 increases on $[t_4, t_3]$ (due to the unfavorable climate conditions) and $p_1(t_4) = p_3(t_4)$. We separate period between t_4 and t_3 in the

season 1.2.1 ($p_1 > p_3 > p_2$, but p_1 decreasing), which distinctive feature is that *although the climate conditions are not comfortable for photosynthesis a plant anyway allocates some part of stored resources to the construction of the vegetative tissues, so as to come into the better conditions with certain amount of already developed vegetative mass.*

Now let there exist some r : $p_1(t) < p_3(t)$ for all $t \in [r, t_4]$. Then a plant enters a storage period. The corresponding equations (8) take a form

$$\begin{cases} \dot{p}_1 = p_1(t)\mu(t) - p_3(t)\nu(t)\frac{\partial f}{\partial x_1}(x_1(t)), \\ \dot{p}_2 = 0, \\ \dot{p}_3 = \omega(t)x_3. \end{cases} \quad (19)$$

If the climate conditions are unfavorable for all $t < t_4$, that is, $p_1(t) < p_3(t)$ for all $t \in [0, t_4]$, then the first period of time is only the storage of allocated photosynthate (this is hardly possible because a seed has a possibility to stay this period in dormancy). If it is not the case, then there exist some moments $t_6, t_5, t_6 < t_5 < t_4$, such that p_1 is decreasing on $[t_6, t_5]$ and $p_1(t_6) = p_3(t_6)$.

We separate the period (t_5, t_4) , which we call period 3.1 (when the climate conditions are disadvantageous and all the allocated material is stored), and time-span (t_6, t_5) called period 3.2 (when the climate conditions are kindly, but all the allocated material is anyway stored "preparation to the unfavorable climate conditions").

Both reproductive and vegetative periods can precede to the storage period. It depends on the climate conditions and values of x^0 . More precisely, from (11), (6) and (10) we have:

$$\begin{aligned} H(t_0) = & g(x_3(t_0)) (v_1(t_0)(\lambda_1 - \lambda_2) + v(t_0)(\lambda_2 - \lambda_3)) + \\ & \lambda_3 \nu(t_0) f(x_1(t_0)) - \lambda_1 \mu(t_0) x_1(t_0) + \lambda_3 \omega(t_0) x_3(t_0). \end{aligned} \quad (20)$$

If $t_0 > 0$, then according to the condition of complementary slackness (12) $H(t_0) = 0$.

It seems that in general we cannot say more about the time of propagation and type of the first period. The reason is that one can choose the values of the initial parameters that are biologically inadequate and consequently obtain unrealistic predictions. For example, if the climate conditions are chosen to be unfavorable for photosynthesis throughout all the time-interval $[0, T]$, then the model is inapplicable, because the strategy to stay in dormancy all the period is not allowed in the model.

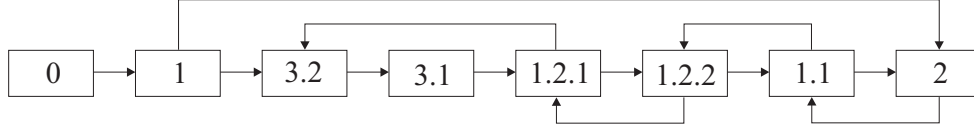


Figure 1: Stages of perennial plant development

To exclude such biologically irrelevant behavior, we consider in the next subsection the case, when the first period after sprouting is vegetative period.

2.3. Predictions of the model

In this section we conclude our investigations. The development of the plant according to the model (1) consists of 3 main periods that can be further subdivided into subperiods and that can follow each other as depicted in the Figure 1.

These periods are:

- 0 - Dormancy.
- 1 - Vegetative period.
- 3.2 - Preparing for the unfavorable climate conditions.
- 3.1 - Life in unfavorable climate conditions.
- 1.2.1 - Allocation to vegetative tissues as a preparation for the climate conditions favorable for the photosynthesis.
- 1.2.2 - A vegetative period that is important for the characterization of monocarpic plants (see below).
- 1.1 Allocation to vegetative tissues before reproduction.
- 2 - Reproduction.

Important special cases of this scheme are:

1. Annual plant with multiple reproduction periods: see Figure 3 (period 1 we identify with 1.1 for simplicity). Multiple reproduction periods appear because of losses of vegetative mass due to external factors that

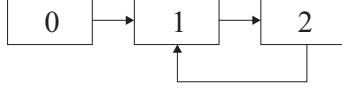


Figure 2: Life-stages of annual plants

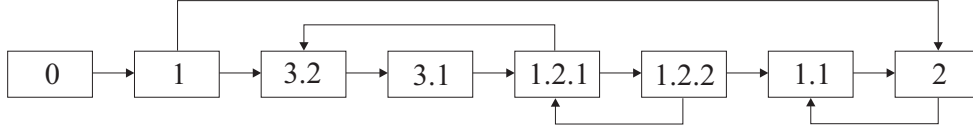


Figure 3: Life-stages of monocarpics

are modeled by the function μ . This particular case has been analyzed in the early work [18]. If $\mu \equiv 0$, then the multiple reproductive periods for annual plants are not possible.

2. Monocarpic plants. Transition $1.1 \rightarrow 1.2.1$ is not possible, see Figure 3.
3. Sufficient (but not necessary) condition for a plant to be monocarpic is negligibility of ω (in particular, if $\omega \equiv 0$), in other words, the mass of storage cannot decrease due to the external factors.

3. Optimization of the seed mass

In the previous sections we have defined fitness of a plant as a mass of reproductive tissues produced by the plant during its life. To maximize the fitness, a plant controls the allocation of photosynthate.

However, it is well-known, that the fitness depends (for plants that propagate themselves with the help of the seeds) crucially on the quantity (and size) of seeds, that a plant produces. Current models of optimal allocation do not provide this information, and a mass of a seed is treated as an external parameter.

3.1. Modeling of seed mass optimization and main result

In this section we consider the model of optimal allocation developed in previous sections and consider the optimal seed size problem for it.

Let $y_0 = (y_1^0, y_2^0, y_3^0)$ be the total mass of the seeds (the vector consisting of the masses of three components of a plant) that has to be divided between a seeds, $a \in [1, \infty)$ and a can be either natural or real number.

We assume that mass of each seed is $s = \frac{y_0}{a}$.

The equations determining dynamics of a plant are as follows

$$\begin{cases} \dot{x}_1 = v_1(t)g(x_3) - \mu(t)x_1, \\ \dot{x}_2 = (v(t) - v_1(t))g(x_3), \\ \dot{x}_3 = \nu(t)f(x_1) - v(t)g(x_3) - \omega(t)x_3, \\ x(0) = \frac{1}{a}y_0. \end{cases} \quad (21)$$

Here $x(0) = (x_1(0), x_2(0), x_3(0))$.

The aim of a plant we define as maximization of the total mass of reproductive tissues produced by all direct descendants:

$$\max_{0 \leq v(t) \leq 1, 0 \leq v_1(t) \leq v(t), a \in [1, \infty)} Q_a = ax_n(T). \quad (22)$$

In contrast to the problem (1), (4) with the fixed mass of the seed, the problem (21), (22) may have no solution (optimality might be achieved for $a \rightarrow \infty$), that is, no admissible controls v , v_1 and parameter a generate the optimal value of $ax_n(T)$.

Recall that a function f is called concave on the set M , if $\forall x, y \in M$, $\forall \alpha \in [0, 1]$ it holds inequality

$$f(\alpha x + (1 - \alpha)y) \geq \alpha f(x) + (1 - \alpha)f(y). \quad (23)$$

If the inequality (23) holds with \leq instead of \geq , then the function f is called convex on the set M .

Important is the case, when f and g are concave functions, that is, the rate of photosynthesis and maximal speed of chemical reactions in a plant are saturated with the growth of the mass of a plant (due to self-shading of leaves, nutrient depletion in the soil etc.).

We have the following result:

Proposition 1. *Let $f, g : \mathbb{R}_+ \rightarrow \mathbb{R}_+$ be concave, $f(0) = g(0) = 0$, $a \in [1, \infty)$. Then $Q_a = ax_2(T)$ increases, when a increases ($x_2(T)$ is a solution of a problem (21), (22)).*

Proof. The problem (21), (22) can be written in equivalent form, using new variables $y_i(t) := ax_i(t)$, $i = 1, 2, 3$. Then we have:

$$\begin{cases} \dot{y}_1 = v_1(t)ag(\frac{y_3}{a}) - \mu(t)y_1, \\ \dot{y}_2 = (v(t) - v_1(t))ag(\frac{y_3}{a}), \\ \dot{y}_3 = \nu(t)af(\frac{y_1}{a}) - v(t)ag(\frac{y_3}{a}) - \omega(t)y_3, \\ y(0) = y_0. \end{cases} \quad (24)$$

The corresponding maximum problem is:

$$\max_{0 \leq v(t) \leq 1, 0 \leq v_1(t) \leq v(t), a \in [1, \infty)} Q = y_2(T). \quad (25)$$

Now the problem is similar to (1), (4), but with $af(\frac{y_1}{a})$ and $ag(\frac{y_3}{a})$ instead of $f(x_1)$ and $g(x_3)$.

Using concavity we have: $f(\frac{y_1}{a}) = f(\frac{1}{a}y_1 + \frac{a-1}{a} \cdot 0) \geq \frac{1}{a}f(y_1) + \frac{a-1}{a}f(0) = \frac{1}{a}f(y_1)$.

Thus, for every $y_1(t) \geq 0$, $a \geq 1$ it holds $af(\frac{y_1(t)}{a}) \geq f(y_1(t))$ and therefore $af(\frac{y_1(t)}{a})$ and $ag(\frac{y_3(t)}{a})$ are nondecreasing in a and $\sup_{a \in [1, \infty)} af(\frac{y_1(t)}{a})$ and $\sup_{a \in [1, \infty)} ag(\frac{y_3(t)}{a})$ yields, when $a \rightarrow \infty$.

Define the value of $y_2(T)$ for a given a as $y_2(T, a)$. Now take arbitrary $n > a$ and consider a system

$$\begin{cases} \dot{y}_1 = v_1(t)ag(\frac{y_3}{a}) - \mu(t)y_1, \\ \dot{y}_2 = (v(t) - v_1(t))ag(\frac{y_3}{a}), \\ \dot{y}_3 = \nu(t)nf(\frac{y_1}{n}) - v(t)ag(\frac{y_3}{a}) - \omega(t)y_3, \\ y(0) = y_0. \end{cases} \quad (26)$$

The solution of this system subject to optimality condition (24) we denote $\hat{y}(t)$. If $\nu(0) > 0$, then from $nf(\frac{y_1(t)}{n}) > af(\frac{y_1(t)}{a})$ we have that $\dot{\hat{y}}_3(0) > \dot{y}_3(0, a)$ and therefore there exists $t^* > 0$: $\dot{\hat{y}}_3(t) > \dot{y}_3(t, a) \forall t \in [0, t^*)$. Hence $\hat{y}_3(t) > y_3(t, a)$ and $ag(\frac{\hat{y}_3(t)}{a}) > ag(\frac{y_3(t, a)}{a})$ for $t \in (0, t^*)$. Let v and v_1 are optimal controls for a system (24). There exist controls $0 \leq \hat{v} \leq v$, $0 \leq \hat{v}_1 \leq v_1$ for a system (26), such that $\hat{v}(t)ag(\frac{\hat{y}_3(t)}{a}) = v(t)ag(\frac{y_3(t, a)}{a})$ and $\hat{v}_1(t)ag(\frac{\hat{y}_3(t)}{a}) = v_1(t)ag(\frac{y_3(t, a)}{a})$. Consequently, $\hat{y}_i(t) = y_i(t, a)$, $t \in [0, t^*)$, $i = 1, 2$. Constructing \hat{v} , \hat{v}_1 for all $t \in [0, T]$, we obtain that $\hat{y}(T) = y(T, a)$ and thus the optimal trajectory of a system (26) produces no less seeds than the best trajectory of (24).

Analogously, the output of the following system is not less than that of the system (26):

$$\begin{cases} \dot{y}_1 = v_1(t)ng(\frac{y_3}{n}) - \mu(t)y_1, \\ \dot{y}_2 = (v(t) - v_1(t))ng(\frac{y_3}{n}), \\ \dot{y}_3 = \nu(t)nf(\frac{y_1}{n}) - v(t)ng(\frac{y_3}{n}) - \omega(t)y_3, \\ y(0) = y_0. \end{cases} \quad (27)$$

Hence $y_2(T, a)$ is nondecreasing in a . □

It follows from the previous proposition that in the case, when f and g are concave the best strategy for a plant is to produce as much seeds as possible.

Similar argument shows that for convex functions f, g the optimal mass of the seed has to be as large as possible (without additional restrictions on quantity of seeds $a = 1$).

Remark 1. *Assuming that f and g are concave and continuously differentiable in the neighborhood of 0 one can investigate $\lim_{a \rightarrow \infty} y_2(T, a)$ using formulas*

$$af\left(\frac{y_1(t)}{a}\right) \rightarrow f'(0)y_1(t) \quad \text{and} \quad ag\left(\frac{y_3(t)}{a}\right) \rightarrow g'(0)y_3(t), \quad \text{when } a \rightarrow \infty.$$

The solution of the obtained linearized problem (with corresponding optimality condition) provides the "theoretical" upper bound for the fitness of the plant under consideration.

Remark 2. *Note that if both f and g are linear, then from (24) it follows that the yield of a plant does not depend on the mass of the seeds.*

The results of this section can be analogously stated also for many other optimal allocation problems. In particular they hold for the model

$$\begin{cases} \dot{x}_1(t) = (1 - u(t))f(x_1(t)), \\ \dot{x}_2(t) = u(t)f(x_1(t)), \\ x_1(0) = x_0, \\ x_2(0) = 0, \end{cases} \quad (28)$$

with optimality condition

$$\max_{0 \leq u(t) \leq 1} Q = x_2(T). \quad (29)$$

Here $x_1(t)$ and $x_2(t)$ are the masses of vegetative and reproductive tissues at time t respectively and f is a monotonically increasing function.

3.2. Discussion of results

We see that the optimal size of a seed depends crucially on the form of the functions f and g . For concave functions that are often used to take into account the self-shading, boundedness of resources etc. (see e.g. [13])

we have proved that according to our model seeds have to be as small as possible.

For the plants living in open environments and for species occupying early phases in succession (colonizing species) the assumption of concavity is not an oversimplification. The behavior that our model predicts, namely that the optimal strategy is to produce a vast amount of small seeds is usual for these species [19].

However, in the closed and shady environments, under mineral shortage, or if there is a strong competition with the established vegetation, the rate of photosynthesis per unit mass can increase with the increasing of a mass of a plant, that is, the function f is convex on some $[0, p]$, $p > 0$ and the seeds cannot be too small. These predictions are, in general, in accordance with experiments [20], [21], but see [22].

Note that similar optimal allocation models can be used also to study life-strategies of the animals, see [23]. In this case it is worth mentioning that there exist species, for which the used in Section 3 definition of fitness (the fitness of a parent is equal to the sum of the fitnesses of all descendants) is not realistic. For example, in recent paper [24] the experimental studies on keelback snakes (*Tropidonophis mairii*, Colubridae) were provided according to which an increase in clutch size increases the offspring size due to the fact that the uptake of water by the snake egg depends upon the number of adjacent eggs. For this case another models have to be constructed and analyzed.

4. Conclusion

In the present paper we have developed the model that describes the optimal allocation strategies of a perennial (as well as annual) plant during all the stages of its life. The model was analyzed with the help of Pontryagin's Maximum Principle, and as a consequence the division of a life of perennial plant (Figure 1) was obtained. The models of monocarpic perennial plant as well as the classic models of annual plant with one or several reproduction periods have been obtained as a special case of the general model.

In the second part of the paper we analyzed the trade-off between size and number of seeds for the optimal allocation problems. We have provided the sufficient conditions that ensure that an optimal strategy is to produce as much (or as less) seeds as possible. The applicability of results has been discussed in the Section 3.2.

5. Acknowledgments

The author thanks Dr. Volodymyr Nemertsalov for fruitful discussions and constructive suggestions.

References

- [1] D. Cohen, Maximizing final yield when growth is limited by time or by limiting resources, *Journal of Theoretical Biology* 33 (2) (1971) 299 – 307.
- [2] T. L. Vincent, H. R. Pulliam, Evolution of life history strategies for an asexual annual plant model, *Theoret. Population Biol.* 17 (2) (1980) 215–231.
- [3] Y. Iwasa, J. Roughgarden, Shoot/root balance of plants: Optimal growth of a system with many vegetative organs., *Theoretical Population Biology* 25 (1) (1984) 78 – 105.
- [4] M. Ziółko, J. Kozłowski, Some optimization models of growth in biology, *IEEE Trans. Automat. Control* 40 (10) (1995) 1779–1783.
- [5] I. Ioslovich, P.-O. Gutman, On the botanic model of plant growth with intermediate vegetative-reproductive stage, *Theoretical Population Biology* 68 (3) (2005) 147 – 156.
- [6] M. De Lara, Mum, why do you keep on growing? Impacts of environmental variability on optimal growth and reproduction allocation strategies of annual plants, *J. Math. Biol.* 52 (5) (2006) 633–666.
- [7] N. Yamamura, N. Fujita, M. Hayashi, Y. Nakamura, A. Yamauchi, Optimal phenology of annual plants under grazing pressure, *Journal of Theoretical Biology* 246 (3) (2007) 530–537.
- [8] D. Takahashi, A. Yamauchi, Optimal Defense Schedule of Annual Plants against Seasonal Herbivores., *The American Naturalist* 175 (5) (2010) 538–550.
- [9] G. Fox, Annual plant life histories and the paradigm of resource allocation, *Evolutionary Ecology* 6 (6) (1992) 482–499.

- [10] F. Bazzaz, J. E. Grace, Plant Resource Allocation, edited volume, Academic Press, 1997.
- [11] E. G. Reekie, F. E. Bazzaz, Reproductive Allocation in Plants, edited volume, Academic Press, 2005.
- [12] W. M. Schaffer, The application of optimal control theory to the general life history problem., *The American Naturalist* 121 (3) (1983) 418–431.
- [13] Y. Iwasa, D. Cohen, Optimal growth schedule of a perennial plant, *The American Naturalist* 133 (4) (1989) 480–505.
- [14] J. Kozłowski, A. Pugliese, Optimal patterns of growth and reproduction for perennial plants with persisting or not persisting vegetative parts., *Evolutionary Ecology* 4 (1990) 75–89.
- [15] A. Alekseev, V. Tikhomirov, S. Fomin, Optimal control (transl. from Russian), Consultants Bureau, New York, 1987.
- [16] C. C. Smith, S. D. Fretwell, The Optimal Balance between Size and Number of Offspring, *The American Naturalist* 108 (962) (1974) 499–506.
- [17] M. Fenner (Ed.), Seeds: the ecology of regeneration in plant communities., 2nd Edition, CABI Publishing, 2000.
- [18] D. King, J. Roughgarden, Multiple switches between vegetative and reproductive growth in annual plants, *Theoretical Population Biology* 21 (2) (1982) 194 – 204.
- [19] J. L. Harper, P. H. Lovell, K. G. Moore, The shapes and sizes of seeds, *Annual Review of Ecology and Systematics* 1 (1970) 327–356.
- [20] A. Jakobsson, O. Eriksson, A comparative study of seed number, seed size, seedling size and recruitment in grassland plants, *Oikos* 88 (3) (2000) 494–502.
- [21] M. Westoby, M. Leishman, J. Lord, H. Poorter, D. J. Schoen, Comparative Ecology of Seed Size and Dispersal [and Discussion], *Philosophical Transactions: Biological Sciences* 351 (1345) (1996) 1309–1318.

- [22] D. J. Metcalfe, P. J. Grubb, I. M. Turner, The ecology of very small-seeded shade-tolerant trees and shrubs in lowland rain forest in Singapore, *Plant Ecology* 134 (2) (1998) 131–149.
- [23] M. Konarzewski, J. Kozłowski, M. Ziółko, Optimal allocation of energy to growth of the alimentary tract in birds, *Functional Ecology* 3 (5) (1989) pp. 589–596.
- [24] G. P. Brown, R. Shine, Beyond size-number trade-offs: clutch size as a maternal effect., *Philosophical transactions of the Royal Society of London. Series B, Biological sciences* 364 (1520) (2009) 1097–1106.